ECOLOGY

Climate change effects on plant-soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems

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Plant-soil feedbacks (PSFs) are interactions among plants, soil organisms, and abiotic soil conditions that influence plant performance, plant species diversity, and community structure, ultimately driving ecosystem processes. We review how climate change will alter PSFs and their potential consequences for ecosystem functioning. Climate change influences PSFs through the performance of interacting species and altered community composition resulting from changes in species distributions. Climate change thus affects plant inputs into the soil subsystem via litter and rhizodeposits and alters the composition of the living plant roots with which mutualistic symbionts, decomposers, and their natural enemies interact. Many of these plant-soil interactions are species-specific and are greatly affected by temperature, moisture, and other climate-related factors. We make a number of predictions concerning climate change effects on PSFs and consequences for vegetation-soil-climate feedbacks while acknowledging that they may be context-dependent, spatially heterogeneous, and temporally variable.

INTRODUCTION

Plants and soils are inextricably linked. Plants alter soil properties, which, in turn, influence plant performance, displaying a variety of effects on each other. These effects of plants on themselves, their offspring, and other plant species through influences on soil organisms and abiotic soil conditions are termed plant-soil feedbacks (PSFs) (*1*–*5*). The interaction between plants and their associated soil biota can lead to complex feedbacks that regulate plant community dynamics and ecosystem processes. The net outcome of PSFs on plant growth depends on the balance between antagonistic and beneficial interactions with the extant plant and soil microbial communities, which can vary depending on both biotic (e.g., plant functional traits) and abiotic (e.g., soil pH, physical structure, and nutrient availability) factors (*6*).

Climate is one of the main drivers of organism growth and species distributions; thus, a changing climate has the potential to alter the composition of plant and soil communities and the interactions between them. However, very little is known about the underlying mechanisms involved and the consequences for feedbacks to climate. In particular, most studies of PSFs have examined the role of soil microbial communities, focusing on net effects of all microbes involved in influencing plant performance positively and negatively (*7*). Identifying the microbial processes that underlie changes in PSFs, such as climate change–induced alterations in the balance of pathogenic and mutualistic taxa or saprophytic microbial taxa that mediate plant nutrient supply, is challenging and requires identifying the individual contribution of the various soil biotic components to PSFs (*8*).

Here, we address the responses of PSFs to climate change and their consequences for biodiversity, ecosystem functioning, and potential feedback effects to climate change. We first consider how soil microbes control PSFs, because the vast diversity of beneficial and pathogenic microorganisms that interact with plant roots or feed on detritus and rhizodeposits can directly affect plant performance (*9*, *10*). We then focus on how climate change may alter primary and secondary succession by affecting PSFs, which are often important drivers of plant species replacement. Soil communities contain a myriad of species that comprise a trophic network of primary producers and consumers, and of secondary and higher-level consumers (*11*) that could be altered by changing climate (*12*). We thus focus on how climate change affects PSFs and soil food webs, with emphasis on both the impacts of increased temperature and climate extremes, especially drought (*12*). We then outline how climate change will affect litterfall and the production of root exudates, which control the structure and dynamics of soil communities. Last, we focus on how increased levels of atmospheric CO_2 directly (i.e., not indirectly via a changing climate) influence PSFs, which will occur simultaneously with its feedback effects to climate.

By discussing PSFs and climate in combination, and the consequences for feedbacks from vegetation-soil to climate, our overriding goals are to anticipate how climate change may affect plant and soil communities, to derive some generalizations about how a changing climate may affect PSFs and consequences for key community and ecosystem-level properties and climate, as well as to identify important knowledge gaps.

MICROBIAL CONTROLS ON PSFs

Soil microorganisms can affect PSFs in complex ways. For example, the accumulation of host-specific pathogenic fungi in the rhizosphere

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is an important driver of negative PSFs, with consequences for plant species coexistence and diversity-productivity relationships (*13*–*15*). Conversely, positive PSFs are typically associated with the accumulation of not only beneficial microorganisms in the rhizosphere, especially mycorrhizal fungi (*16*–*17*), but also nitrogen (N)–fixing symbionts (*18*–*19*). PSFs can also become more positive or less negative because of free-living soil bacteria and fungi involved in the decomposition of organic matter (*20*) and the transformation of plant growth–limiting nutrients (*21*).

Recent evidence suggests that PSFs involve myriad interactions among a diversity of beneficial and antagonistic microbes. For example, the same graminoid microbial [arbuscular mycorrhizal (AM) fungi] partners can shift from beneficial to antagonistic depending on microsite conditions (*22*). Similarly, although AM fungi are often beneficial to trees (*23*), tree species with AM fungi have also been shown to more often experience negative feedback in comparison to ectomycorrhizal (EM) trees, which predominantly display positive feedback (*24*, *25*). In addition, studies reveal that these effects of soil fungi on PSFs vary across fungal guilds (*26*): Feedbacks might become more negative as the richness of plant pathogens and specialist decomposers increases and become more positive as the diversity of AM fungi increases (*25*, *26*). These studies show that PSFs may depend on plant interactions with highly diverse rhizospheric microbial communities rather than with single host-specific pathogens or mutualistic symbionts (*14*, *25*, *26*).

Climate change can modify the direction and intensity of microbial-mediated PSFs through a variety of mechanisms. For example, the alteration of soil microbial communities by climatic extremes, such as recurring droughts, can modify both the direction and intensity of PSFs, with consequences for plant-plant interactions and invasiveness (*21*, *27*–*28*). The adaptation of soil microbial communities to drought can also improve plant fitness (*29*) and favor mycorrhizal fungi and symbiotic soil bacteria, which enhance the tolerance of plants to drought (*30*) and presumably influence PSFs. Warming and altered precipitation will also modify PSFs, hence plant-plant interactions, by altering belowground pathogen pressure and root associations with mutualistic symbionts and/or by decoupling range-expanding plants from their host-specific soil communities, including pathogens (Fig. 1) (*31*). Changes in plant physiology and phenology caused by climate change, although poorly understood, can alter soil microbial communities via changes in rhizodeposition (i.e., the release of resources from plant roots into the soil), thereby potentially modifying the microbial-mediated PSFs (*32*, *33*) and the capacity to change feedback effects from soil and vegetation to climate.

Evidence suggests that climate change may affect the biodiversity and function of soil microbes. Rainfall timing plays a critical role on the abundance and diversity of soil microbial populations in grasslands (*34*), and the diversity of microbial gene functions in topsoil microbial communities is strongly correlated with precipitation, suggesting a clear association between specific microbial metabolic functions and climate (*35*). Drought legacy effects influence the composition of soil fungal and bacterial communities via specific response groups composed of members with broad phylogenetic origins, including rare taxa (*36*). This suggests that rare taxa should not be overlooked when modeling microbial responses to climate change and their potential consequences for plants.

Key microbial processes involved in potential change of PSFs are context dependent and differ across ecosystems and with the plant species involved. However, some generalities are beginning to emerge that could help enhance our capacity to predict PSFs and vegetation dynamics in terrestrial ecosystems (Table 1). For instance, some studies show a consistent role of mycorrhizal type in influencing PSFs at multiple scales (*24*) and reveal the importance of plant traits, especially those related to nutrient acquisition strategy, for explaining PSFs (*19*, *28*). Furthermore, while it is unknown as to how interactions between plants and soil biotic communities will evolve in response to proxies of climate change, it is likely that they will affect the outcome of PSFs with potential consequences for vegetation dynamics, ecosystem processes, and feedback effects to climate. For example, drought can alter soil bacterial and fungal communities and modify the direction of PSFs and plant competitive interactions (*21*); soil bacterial communities in the tropics and at high latitudes are subjected to stronger environmental filtering and include more edaphic-niche specialists, possibly rendering these communities more vulnerable to global change (*35*). As such, climate change is likely to have both strong direct effects on plants and soil organisms, as well as indirect effects through changes in plant physiology and the quality and quantity of resources entering soil (i.e., as litter and rhizodeposits) (Fig. 2). This will, in turn, have potentially large consequences for PSFs, vegetation dynamics, and feedback effects to local or even global climate conditions. In sum, and despite the complexity and high variety of processes involved, our ability to make predictions involving PSFs is improving, and in the future, it should increasingly be possible to apply this knowledge to address environmental challenges such as climate change mitigation or ecosystem restoration by using nature-based solutions, as well as informing conservation policies.

TEMPERATURE AND DROUGHT EFFECTS ON PLANT-SOIL INTERACTIONS

Climate change alters plant-derived inputs to soil in the form of litter production and rhizodeposition, raising questions about the way and intensity with which they are affected (*37*, *38*). If terrestrial plant productivity does increase with warming by increasing nutrients available from decomposition, then more litterfall may be expected. However, higher temperatures affect plant physiology and lead to higher evaporation and plant transpiration, exacerbating water shortage effects. In addition, acclimation to warming is likely to dampen potential responses. Climate change is also expected to increase the intensity and frequency of climate extremes, for instance, through increased drought periods and periodically extreme rainfall conditions. Some studies simulating moderate drought conditions in extratropical ecosystems counterintuitively found an increase in aboveground litter production, but only in the short term (*39*). By contrast, studies from humid and subhumid tropical forests found no changes or only slight decreases in the production of aboveground litter under moderately induced drought (*40*). Persistent drought, however, leads to species turnover and less aboveground biomass, resulting in less litter production (*39*, *40*). Increasing aridity in geographical gradients also results in decreased aboveground litter production (*41*). The quality of litter decreases with drought in all biomes, even if total litterfall remains constant, partly because of elevated nutrient resorption prior to leaf senescence (*42*) and the production of carbon-based, recalcitrant structural compounds under drought (Fig. 2). These changes not only slow down mineralization rates, nutrient release, and nutrient cycles that may increase or decrease plant diversity through species turnover, depending on environmental conditions (*43*, *44*), but also affect CO_2 release to the atmosphere and therefore feedback to climate.

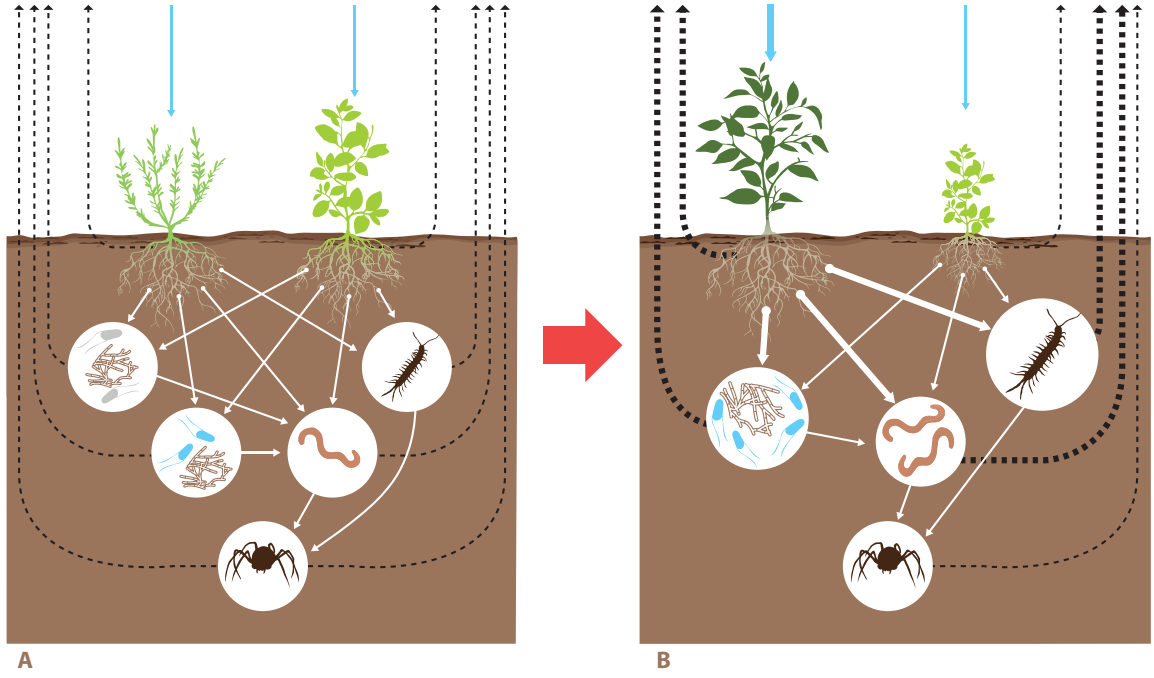

Fig. 1. Alteration of trophic relationships depending on responses to climate change. Arrows indicate CO_2 flow; solid arrows represent net input, and dashed arrows represent net output, with arrow thickness proportional to flow. Circles show different species in a simplified soil food web. The unperturbed system prior to the onset of a chronic global change driver (**A**) gives way to a long-term response (**B**) in which poorly performing plant species and their pathogens or symbionts are lost from the system, and new, more competitive plant species that have escaped their natural enemies are added to the community. As a result, the biomass of nonspecialist mutualists or pathogens increases, and the biomass of one decomposer group remains high [modified from (*37*)].

Table 1. Summary of expert assessment of potential impacts of climate change drivers (positive, negative, or neutral) on PSFs based on the general effects of known environmental conditions on soil communities.

PSF type	Climate change drivers				
	Warming	Drier conditions	Wetter conditions	Fire	Increased CO_2
Fungi					
Pathogens	+++	−−	+++	−−	0
Saprotrophic/organic matter decomposers	++	−−	+++	−−	?
AM fungi	+++	+++	+	−−−	?
EM fungi	+	−−−	+	−−−	+
Bacteria					
Pathogens	+++	−−	+++	−−	?
Symbiotic N fixers	0	−−−	++	0	+
Nonsymbiotic N fixers	0	−−	++	0	+
Drought-tolerant microbes	+	+++	−−	0	?
Other specific coevolved microbes	+++	−−−	++	++	?
Other					
Primary detritivorous invertebrates	++	−−	++	−−	?
Secondary detritivorous invertebrates	++	−−	++	−	?
Root herbivores	++	−−	++	0	?

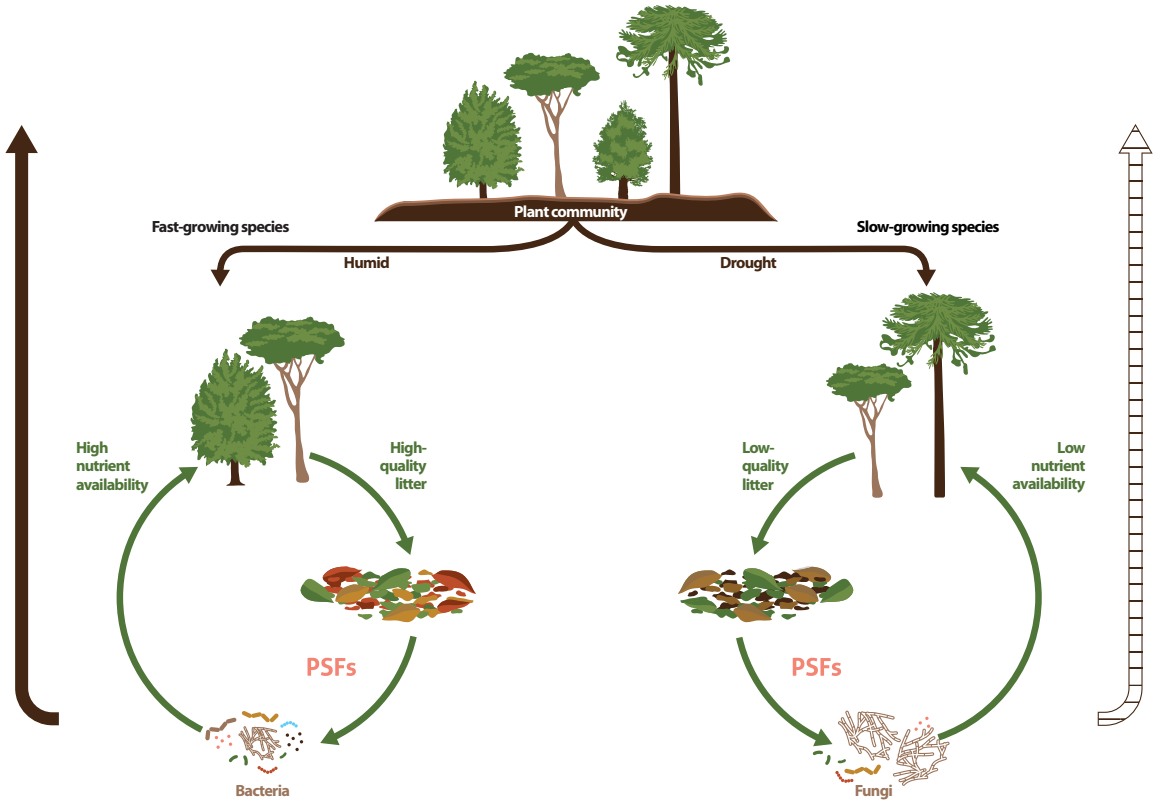

Fig. 2. Effects of drought on litter productivity and species turnover and their relationships with PSFs. Drought leads to low-quality litter with recalcitrant carbon (C) compounds and low nutrient content. This litter is difficult to decompose and determines a fungal-dominated microbial community composition while decreasing the availability of nutrients for plants. These conditions lead to a replacement by plant species that are better adapted to drought conditions, in contrast to more humid conditions where nutrient-rich litter is fast decomposed by bacterial-dominated microbial communities. Arrows indicate carbon flow; solid arrows represent net input, and dashed arrows represent net output, with arrow thickness proportional to flow.

Increasing aridity can cause large changes in nutrient cycling and enhances the impact of ultraviolet radiation on litter decomposition (*45*, *46*), which may cause an imbalance in nutrient cycling with negative effects on plant diversity (*47*). Decreases in plant growth and belowground carbon allocation in grasslands as a consequence of drought have also been reported (*48*), and drought has legacy effects on soil microbial communities that can affect plant-plant interactions (*21*) and even neutralize PSFs through increased water demand linked to higher nutrient demand with positive PSFs (*28*). In dry ecosystems, soil microbes can buffer the negative effects of drought on seed germination and plant growth in a species-specific way, so that plants such as legumes that are more dependent on specific coevolved microbes are more sensitive and less buffered by soil microbiota than other species (*49*). PSFs also play a key role in plant recruitment by influencing seed germination and seedling establishment, which are, in turn, important in regulating plant diversity and community dynamics (*14*). The susceptibility of different plant species to soil biota determines their relative abundance, as soil pathogens reduce recruitment and survival of different species (*2*). In contrast, other soil microorganisms offer protection from pathogens or modify nutrient availability, thereby benefitting some plant species over others (*7*). Our knowledge on how PSFs can affect plant communities and ecosystem dynamics can help us forecast potential trajectories of ecosystem change under different climate change scenarios.

PSFs AND FOOD WEB DYNAMICS

Microbes are part of a complex soil food web, which consists of numerous species or taxa across different trophic levels, including primary producers (plant roots and algae), primary consumers (bacteria, archaea, fungi, viruses, and root-feeding fauna), and secondary and higher-level consumers (bacterivores, fungivores, and predators) (*10*, *50*). These organisms are all important components of the plant-soil system that are able to alter the outcome of PSFs (*51*). Although widely acknowledged as important drivers of soil biogeochemical processes modulated by climate (*52*), soil food webs show high interactivity and complexity (*11*). Climate change effects on soil food webs will be affected by the fact that combined responses of the individual components of PSFs—decomposers, mutualistic symbionts, and herbivores/pathogens—are all influenced (Fig. 3) (*7*). However, the net effects will be difficult to predict when we consider all the individual components of the soil biota in isolation. The elegance of the PSF concept is that the overall functional consequences of climate change on the soil biota can be assessed through its combined impact on plant performance and, ultimately, the net PSF effect. This may also have implications for extremely long-term patterns in PSFs. For example, body size of soil invertebrates decreased during the dry and warm conditions in the Paleocene-Eocene Thermal Maximum, affecting ecosystem functions such as organic matter decomposition and nutrient cycling, which, in turn, affected plant diversity (*53*). The consequences of these long-term effects on the soil food web

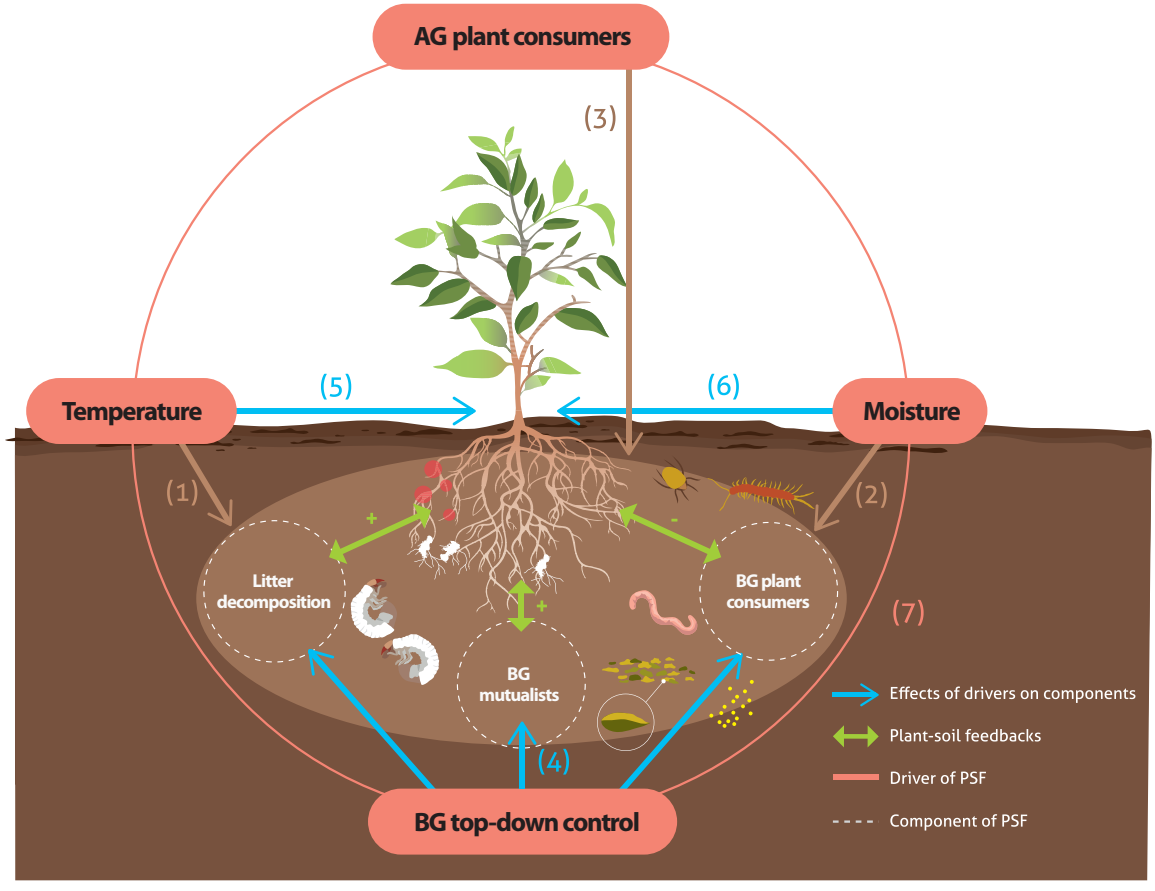

Fig. 3. Depiction of effects of abiotic and biotic drivers on PSFs. Drivers such as temperature (1), moisture (2), aboveground (AG) plant consumers (3), and belowground (BG) top-down control (4) impact on several components of PSFs (e.g., BG mutualists, plant consumers, and litter decomposition) are shown. Orange ovals show the abiotic and biotic drivers of PSF components, shown in dashed circles. PSF components control whether the feedback response is positive or negative. Temperature, moisture, and aboveground plant consumers can also directly affect plant performance (5 to 7). Abiotic and biotic drivers could interact with each other (circle connecting the drivers), and this will affect the way that each one affects the components of PSFs [based on (*108*)].

for PSFs have not yet been assessed. The influence of climate change may also affect plant community composition through mechanisms such as shrub encroachment, as discussed in the section on succession.

If water and nutrients become limiting, the role of mutualistic symbionts in the soil food web, which are involved in plant nutrient acquisition and drought tolerance, may increase: AM fungi and N fixers both lead to positive PSFs, which can promote primary production if all other conditions remain unaltered (*54*). This scenario may also affect plant community composition, with an increased dominance of plant species that fix N and/or those forming AM (*55*). These plant species, however, are not necessarily less influenced by soil-borne pathogens (*24*), and PSFs may easily become more negative, because climatic extremes may increase the vulnerability of plants to herbivores or pathogens (*56*).

PSFs AND RANGE EXPANSION

An important element of climate change is range shifts of plants, soil animals, and microbial taxa over time (*12*, *35*). Range-shifting plant species have fewer negative PSF effects in their new range (*57*). Few studies have compared PSF effects between the original and new ranges but suggest that range shifts enable plant species to become released from negative PSFs (*58*). In the new range, PSFs are expected to become more negative over time because of pathogen accumulation (*59*); in the meantime, range-shifting plant populations may have invasive characteristics and potentially reduce local native plant biodiversity (*60*). Range shifts seem to have much weaker effects on plant-mutualist symbiotic relationships and plant-decomposer interactions than on other plant-microbe interactions, possibly due to the lower degree of host specificity of these microbes. Thus, direct effects of climate on temperature and rainfall, along with species range shifts, are likely to affect PSFs. PSFs during range shifts under climate change will most likely turn from negative in the home range to less negative, or even positive in the new range. However, these effects can be dynamic when considering longer time periods and are ultimately expected to become more negative over time because of cointroduction of the native pathogens or evolutionary developments of local pathogens (*60*).

The type and timing of climatic extremes may be crucial for the dynamics and range expansion of plant communities. Drought or extreme rainfall may occur before or during the growing season, and their effects on plant community composition can differ. In a greenhouse study (*27*), plant species that expanded their range from southern Europe (warm and dry) toward northern Europe (currently

warming) were grown in mixed communities with their congeneric relatives that were native to northern Europe. The soils in that study had been subjected to preseason drought, preseason rainfall, and combined conditions and were then brought back to control soil water conditions. Preseason drought increased the proportional contribution of range-expanding plant species to community composition, whereas preseason rainfall had smaller effects (*27*). These effects corresponded to the increased abundance of the so-called "drought response types" or "wet response types" among both bacteria and fungi (*36*). Furthermore, a recent outdoor mesocosm study (*61*) compared the current climatic situation with three future scenarios: range shifts of plants but not soil biota, range shifts of soil biota but not plants, and range shifts of both plants and soil biota. During the growing season, half of the mesocosms were exposed to drought, while the other half was provided with the 30-year average water conditions of nondrought years. During extreme drought, decomposition was strongly reduced in all four types of mesocosms. After rewetting the soil, however, decomposition with plants in temperate zones recovered 2 weeks faster than that with range-shifted plants that originated from a region characterized by severe summer droughts.

Recent evidence suggests that range shift of plant species as a consequence of climate change may be essential for the adaptation of ecosystems to novel climatic conditions (*62*). However, when range-expanding plant species have invasive properties, they may change ecosystem processes, for example, through altered nutrient cycling and interactions with above- and belowground biota (*63*). Moreover, range expanders may also respond differently to extreme weather events than will native plant species. Managing these types of changes in ecosystems will be crucial, and the maintenance of soil biodiversity is expected to ensure soil functioning under a variety of novel climatic conditions (*50*).

LITTER TRAITS AND DECOMPOSITION UNDER CLIMATE CHANGE

Climatic factors, such as temperature and rainfall, are critical controls of litter decomposition, and these factors interact with local plant and soil communities (*64*, *65*). Relationships based on climatic averages conceal much of the local variability, and the response of this local variability to climate change will determine how climate change is likely to influence global patterns of litter decomposition (*66*).

The turnover of plant species due to climate change can greatly affect litter decomposition (Fig. 2) (*67*). Field and laboratory experiments have shown that litter quality determines the functional characteristics of the soil decomposer community. Recalcitrant litter can contain considerable amounts of polyphenols (e.g., phenolic acids and flavonoids) or polymers (e.g., condensed tannins) that require high activation energy (*68*) and inhibit microbial decomposition (*69*). Recalcitrant litter would, however, promote microbial communities specialized in degrading complex plant polymers (*70*), so slow microbial metabolism and nutrient release will favor slow-growing plant species. Furthermore, under warmer and drier conditions, fungal metabolism can shift toward maintenance at the expense of the production of enzymes that break down plant-carbon compounds, with concomitant effects on plant communities and ecosystem carbon dynamics (*71*). Under different scenarios, it is likely that communities dominated by fast-growing species will continue to produce high-quality litter, which may promote soil microbial communities that will decompose litter at faster rates (*72*), maintaining high soil nutrient availability where fast-growing species thrive (Fig. 2).

In addition to leaf litter, rhizodeposition is a large source of organic matter entering the soil that will be affected by climate change. Rhizodeposits are highly dependent on plant physiological activity, which will be affected by expected changes in climate. Changes in exudate composition, not just quantity, may also have crucial impacts on soil properties and organisms. Under drought, plants exudate more secondary compounds (including antioxidants), phytohormones, soluble sugars and compounds that act as osmolytes (*73*, *74*), as well as metabolites such as proline (*75*) that buffer the cellular redox status during drought. Drought-driven changes in rhizodeposition, thus, have complex effects on bacterial and fungal communities. The changes depend on the intensity of the drought and previous soil history. Bacteria may be more negatively affected than fungi in terms of biomass stock. The resulting shift toward a relative increase in fungi and a relative decrease in the biomass and diversity of bacteria (*76*) is likely to affect food webs and plants by generating different availabilities of nutrients (*43*). In addition, altered microbial communities would feed back to the extant plant community through altering organic matter decomposition (*77*, *78*) and nutrient uptake (*79*), likely leading to different patterns of species replacement. Thus, climate change impacts on plant-soil interactions will have consequences for the carbon cycle, and a potential decoupling of plant-soil interactions may happen as if plants undergo a range shift while their associated soil communities do not. This decoupling is a largely unrecognized, but potentially important, regulator of the future global carbon cycle (*37*).

HOW CLIMATE AFFECTS PSF CONTROL OF SUCCESSION

PSFs are often important drivers of plant species replacement and, thus, succession, which includes impacts of both soil biota associated with plant roots and those involved in the decomposer subsystem (*80*). Given that disturbance associated with climate change may increase in the future (e.g., more fires, more windthrow), impacts on, and consequences of, PSF-driven succession will likely increase in importance. Feedbacks between early successional plant species and their root-associated soil biota frequently contribute to the replacement of these species by other species. This replacement may arise, for example, by early successional species promoting the accumulation of soil pathogens that negatively affect them (*4*, *81*) or by forming mutualisms with symbiotic N-fixing bacteria that improve soil fertility and thereby facilitate later successional species that outcompete them (*82*). By contrast, late successional species often form positive associations with their soil biota and, notably, with mycorrhizal fungi, which slows succession. For example, along a chronosequence of Dutch (old field) grasslands on abandoned arable land, early successional plant species consistently underwent negative feedbacks with their soil biota, while late successional plants only underwent positive feedbacks (*83*). PSFs involving soil biota can also alter plant succession by altering the supply of soil nutrients available to plants. Decomposer biota can thus accelerate succession by mineralizing nutrients that facilitate later successional species that then outcompete earlier species (*84*), or succession can be retarded if plants produce recalcitrant litter that can be better metabolized by their own mycorrhizal symbionts than by those of other species (*85*, *86*).

Although we have some understanding of how PSFs influence plant succession, we have limited knowledge on how these effects

are mediated by climate or how they might be altered by ongoing climate change. Explicitly addressing this issue will require studies that directly consider the interactive effects of macroclimatic variables and succession; few studies have used such an approach (*87*–*89*), and none of them have explicitly studied PSFs. However, the work by Laliberté *et al.* (*89*) does offer some insights. Here, plant biomass and the structure of the soil food web were investigated across each of the four parallel chronosequences formed on the same parent material in Western Australia; these four sequences differ in both temperature and moisture balance within the range of what would be expected for future climate change. They showed that chronosequence stage was the most important driver of the soil food web, with little interactive effect of stage with climate. Given that the soil food web governs nutrient supply rates from the soil, which then affects successional processes, this study suggests that variation in the ecological impact of the soil food web and, ultimately, its impacts of PSFs among (versus within) successional gradients of contrasting climate is probably not large. This study does not, of course, directly address the question about how climate determines the role of PSFs in driving succession, and it remains unknown whether the results of this study are likely to apply to successional gradients elsewhere, but it offers insights into how this question could be explicitly addressed.

At a broad level of resolution, the types of above- and belowground biotic changes that occur during succession and ecosystem development appear to be relatively constant among regions that experience very different climatic regimes (*89*–*91*). Therefore, the biggest effects of climate change in driving how soil biota and PSFs affect succession are likely to be driven by finer-scale factors such as what types of plants in any given environment will or will not be favored by future climate. For example, shrub encroachment of subarctic tundra resulting from climate change (*92*) involves successional pathways moving toward domination by woody plants that show positive feedbacks with ericoid and EM fungi. Conversely, in some temperate regions, warming should lead to successional pathways involving domination by trees that undergo feedbacks with AM fungi rather than with EM and saprophytic fungi (*93*). Increasing aridity in tropical regions may promote early successional species that form positive associations with N-fixing bacteria (*94*, *95*), thereby eventually benefitting later successional species. There are numerous examples of where specific plant functional types are likely to enter or exit successional pathways due to climate change, and while each of these will have their own feedbacks with their associated soil biota, the nature and direction of these feedbacks are likely to be case specific. Understanding the mechanisms underlying this context dependency is key to understanding and predicting how successional pathways develop under a changing global climate and, therefore, the dominant types of vegetation that are likely to result.

PSF RESPONSES TO ELEVATED CO_2

We have so far referred mostly to climate, but the direct effects of elevated CO_2 (eCO_2) may be important as well. In addition, any effect of climate change on PSFs will happen within the context of rising CO_2 effects on PSFs; hence, consideration of both direct CO_2 and direct and indirect effects of climate change seems essential to develop a holistic, integrated perspective. A critical question involving the impacts of eCO_2 on PSFs is whether eCO_2 stimulates the soil community to increase the rates of decomposition and associated N and phosphorus (P) cycling through increased plant productivity, or has neutral or negative effects on decomposition and nutrient cycling. The former PSFs allow the responses of plant biomass to eCO_2 to remain stable or grow stronger (the "priming" effect), whereas the latter PSFs contribute to, and perhaps increase, the extent of the constraints of nutrient limitation on the use of eCO_2 by plants. This is a major puzzle in eCO_2 science because many kinds of effects, for instance, increased, neutral, or decreased soil nutrient cycling in response to eCO_2, have been reported (*96*–*98*). This puzzle is also a key issue for society, and the questions of whether or how much the direct effects of eCO_2 stimulate a negative feedback from terrestrial ecosystems that reduces the rate of global warming [by additional carbon (C) sequestration] are poorly understood. This sequestration requires an increase in C uptake by plants and a neutral, negative, or positive return of C to soil (by autotrophic and heterotrophic respiration) that is smaller than the uptake. Soil microbes play a key role both because they control the supply of nutrients to plants and thus the magnitude of increase in the response of biomass to eCO_2 and because they determine the rate of decomposition of both new and old C in soils.

Organisms at higher trophic levels play a role in the soil food web, but two groups of soil microbes have particularly important roles in these processes and, thus, in the responses of terrestrial ecosystems to eCO_2: the mutualistic mycorrhizal fungi and heterotrophic decomposers (*99*). Their characteristics and tendencies may help us solve the puzzle of the eCO_2 responses outlined above. They are important because (i) nutrient limitation on plant responses to eCO_2 may be modulated by the type of nutrient-acquisition strategy, which, in turn, may be largely determined by mutualistic symbiotic plant-microbe interaction, and (ii) eCO_2 may increase nutrient cycling or have neutral or suppressive effects due to the regulation by and impacts on both mycorrhizae and decomposer communities.

Plant species associated with EM fungi have a stronger response of biomass to elevated eCO_2 when soil has more available N, whereas plant species associated with AM fungi increase biomass more under eCO_2 when soils have more available P (*100*). These responses are partly due to the lower cost and thus higher return on investment for acquiring additional N under eCO_2 when associating with EM rather than AM fungi (*100*). EM plants, however, decrease soil C pools via priming (i.e., the stimulation or suppression of soil organic matter decomposition by live roots and associated rhizosphere organisms) (*99*), offsetting the scope of their potential increased C sequestration induced by eCO_2.

Long-term eCO_2 also influences soil decomposer communities in ways that likely influence decomposition and the potential storage of soil C. For example, eCO_2 in a long-term eCO_2 experiment in perennial grassland led to distinct microbial communities (*101*). The abundances of key C-fixation genes; some C-degrading genes involved in the decomposition of starch, cellulose, and hemicellulose; and functional genes involved in N cycling were also higher (*102*, *103*). These changes in soil microbial communities and their functional genes and enzymatic production likely play key roles in the faster decomposition of soil organic matter under eCO_2.

Our understanding of whether or how eCO_2 will drive complex interactions of soil communities in space and time remains limited, despite the considerable advances briefly outlined above. For example, a 20-year free-air CO_2 enrichment study found that the impact of eCO_2 on microbial-mediated nutrient cycling and, consequently, on the responses of biomass to eCO_2 can change over time in ways unpredicted by theory because of poorly understood mechanisms

(*103*). The impacts of eCO_2 on soil N cycling in this study shifted from positive to negative over time in C3 grass communities and from negative to positive over time in C4 grass communities. These shifts in N cycling contributed to parallel shifts in the responses of biomass to eCO_2; biomass enhancement due to eCO_2 disappeared over time in the C3 grass communities and increased over time in the C4 grass communities. Changes in the composition, abundance, and function of both mycorrhizal and decomposer communities likely played influential roles in these temporal shifts, but we have neither the empirical evidence to characterize that pattern nor a sufficient theoretical foundation to conceptually explain it convincingly. The possibility that long-term changes in soil communities, including their responses to eCO_2 and cascading biogeochemical impacts, may follow a diversity of possible pathways that are broader than we have anticipated suggests that we should be cautious in our confidence to predict these interactions, or their consequences, in the long term. This caution becomes even more apparent when we consider the potential interactions among eCO_2, temperature, and/or moisture on soil communities and PSFs (*104*, *105*).

UNSOLVED QUESTIONS

Understanding the mechanisms underlying the context-dependent nature of PSFs is critical for understanding and predicting how pathways of succession and range shifts develop in terrestrial ecosystems under a changing global climate and, therefore, the types of species that are likely to dominate the plant communities. It is also of importance for predicting how climate change will affect ecosystem processes, including potential carbon cycle feedbacks at different spatial scales. How climate change affects decomposers, mutualistic symbionts, and pathogens, and their net effects on PSFs needs further study; although these effects are heavily context dependent, certain general patterns are emerging. Identifying the specific microbial and food web processes, including changes in the abundance of key taxa, microbe-microbe and microbe-invertebrate interactions involved in nutrient supply, and trophic interactions within soil food webs, is needed to determine the underlying drivers and mechanisms underpinning this context dependency (*106*). Furthermore, little is known about the possible role of viruses in PSFs and their sensitivity to climate change. Further studies are needed to understand how warming and changes in precipitation affect these interactions, including the importance of rhizodeposits, which are often overlooked in studies of decomposition.

Similarly, important gaps remain in our understanding of specific aspects of climate change, such as the relative and interactive effects of warming and CO_2 enrichment on these links, and how they are influenced by the rapidly increasing extreme meteorological events such as drought, floods, and altered freeze-thaw cycles. Last, further studies are needed to determine how PSFs can be promoted to control potential invasiveness of range-expanding native and introduced exotic alien plant species or their use in practical issues such as nature-based solutions or natural climate solutions (*107*). Understanding how climate change influences succession requires an understanding of how the effects of PSFs on succession respond to climate. Addressing this issue requires studies that explore the interactions of climate and succession, and there is a dearth of these studies at present.

However, and despite the many uncertain responses of PSFs to climate change, we can already draw a number of conclusions:

1. As the types of above- and belowground biotic changes that occur during succession are relatively constant across regions with very different climates, we predict that the role of PSF in succession might not be greatly altered by climate change.

2. However, how plant functional types exiting or entering successional pathways respond to climate change and the role of PSFs in mediating this response are likely to be case specific.

3. Enhancing the sustainability of ecosystem function both above- and belowground may require promotion of the fungal component in soils because soils dominated by fungi are more stable under extreme droughts and more able to retain nutrients, which thus limits nutrient losses from soil.

4. Climate change–induced shifts in plant distribution may enable plants to become released from negative PSF for a prolonged period (decades or longer). In their new range, some range-shifting plant species therefore may show invasive dominance.

5. Extreme weather events resulting from climate change may also alter PSFs in such a way as to promote the dominance of introduced exotic species.

6. Invasive species outbreaks fostered by climate change may be controlled by negative PSFs in biodiversity-rich ecosystems.

7. Climate change impacts on PSFs will have consequences for the carbon cycle at local scales, although their role as a regulator of carbon cycle feedbacks at larger scales remains uncertain.

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Acknowledgments

Funding: F.I.P. was supported by the Spanish Research Agency (grant CGL2017-84515-R). J.P.'s research was funded by the European Research Council Synergy grant (ERC-SyG-2013-610028, IMBALANCE-P). A.G. was supported by FONDECYT-Chile 1160138 and CONICYT AFB 17008. P.B.R.'s research was supported by the National Science Foundation (NSF) grants DEB-1831944 and DEB-1753859. **Author contributions:** F.I.P. took the initiative and led, and all coauthors contributed equally to the writing of the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper. Additional data related to this paper may be requested from the authors.

Submitted 19 August 2019
Accepted 28 October 2019
Published 27 November 2019
10.1126/sciadv.aaz1834

Citation: F. I. Pugnaire, J. A. Morillo, J. Peñuelas, P. B. Reich, R. D. Bardgett, A. Gaxiola, D. A. Wardle, W. H. van der Putten, Climate change effects on plant-soil feedbacks and consequences for biodiversity and functioning of terrestrial ecosystems. *Sci. Adv.* **5**, eaaz1834 (2019).

Science Advances

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Sci Adv **5** (11), eaaz1834.
DOI: 10.1126/sciadv.aaz1834